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## A NEW PHYTOSAUR FROM THE TRIAS OF ARIZONA

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Among the vertebrate remains from the Triassic of the western states no other group is so abundantly represented as the Phytosauria. Relatively abundant as fossils of this group are, however, there is much to be learned of each of the several distinct types that have been described. For the most part it is the skull that is available for study, but even this is imperfectly known.

Some time ago the writer described a well-preserved phytosaur skull from Arizona, now in the geological museum of the University of Wisconsin. This skull was considered a new form and was made the type of the genus *Machaeroprotopus*.<sup>1</sup> While several of the doubtful details of the phytosaurian skull were made known by the study of the specimen, especially the relations of the bones of the posterior side, the palate, as is usually the case, was left in doubt.

Through the kindness of the University of Chicago the writer was permitted some time ago to study a phytosaur skull in the collections of Walker Museum; a skull very similar to the University of Wisconsin specimen in many points. The study of this material has made evident several pointed suggestions especially concerning the structure of the palate.

The specimen herein described is No. 396 of the Walker Museum Vertebrate Paleontology Collections. It is the gift of Professor J. E. Anderson, formerly of the School of Mines, at Socorro New, Mexico. The name of the collector is unknown and the exact locality has not been recorded. However, the skull is known to

<sup>1</sup> M. G. Mehl, "New or Little-known Reptiles from the Trias of Arizona and New Mexico, with Notes on the Fossil-Bearing Horizons near Wingate, New Mexico," *Bull. University of Oklahoma*, New Series No. 103, University Studies Series No. 5, 1916, pp. 5-24.

have come from the Triassic of Guadalupe County, near Santa Rosa, New Mexico.

The material collected consists of a few large, well-preserved pieces of bone representing a fairly complete skull (Fig. 1). In the skilful hands of Paul C. Miller the missing portions have been restored in plaster and the major features are almost as certainly determined as though all the fragments had been collected. On both the dorsal and the ventral sides the skull is complete along the median line save for the occipital condyle proper. On the right side the jugal, except for the portion that forms the posterior border of the antorbital fenestra and the process that takes part in the border of the orbit, is missing, as is the quadratojugal, the squamosal, and all but the anterior end of the postorbital. On this side, too, the outer end of the paroccipital and the quadratopterygoid bar are missing. On the left side the missing portions are much the same as on the right, except that the restoration extends farther forward. On the left side the posterior end of the jugal and all of the quadratojugal are preserved.

The skull (Fig. 1) is large, about 865 mm. long, and massive. It is a crested form of the "broken outline" type. From an oval cross-

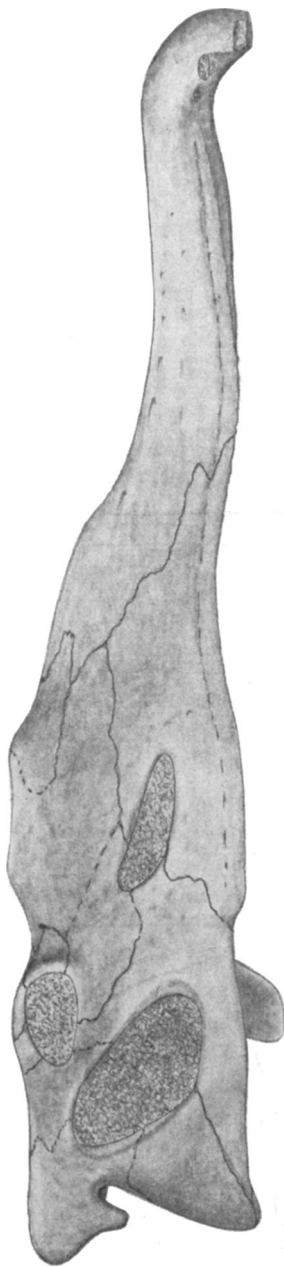


FIG. 1.—*Machaeroprotopus andersoni*, side view of restored skull, slightly over one-sixth natural size. Sutures indicated by broken lines cannot be determined.

section just behind the expanded and abruptly downturned tip, the rostrum gradually assumes an A-shaped cross-section. Back from the tip for a distance of about 293 mm. the rostrum does not increase in depth materially. At this point, however, the outline of the crest bends in a pronounced curve upward for a short distance and then extends in an essentially straight line up to the anterior border of the nares, 512 mm. from the tip of the rostrum. As the crest approaches the nares after the abrupt rise, it loses much of its angular cross-section.

The narial 'hump,' while actually rising above the plane of the cranium proper about half an inch and while somewhat accentuated by the depression of the cranial roof in front of the orbits, is not so conspicuous as in several other forms. This is due to the fact that the crest is but slightly depressed immediately in front of the nares.

#### OPENINGS OF THE SKULL

The position of the *nares* is that of the most highly specialized phytosaurs, high on the skull and not far from the eyes. The posterior border of the nares is about 105 mm. in front of the center of the orbit. The openings are 63 mm. long and about 21 mm. wide. They are separated by a moderately thin partition that does not reach the level of the outer borders. The plane of the combined openings is directed upward.

The *orbits* are slightly longer than wide, about 62 mm. in diameter.

The *antorbital fenestrae* are somewhat distorted. They appear to have been about 104 mm. long and perhaps 45 mm. wide. While they do not extend forward beyond the nares, as is the case in similar forms, this is due to the moderate length of the antorbital fenestrae and not to a unique position.

The sides of the *lateral temporal fenestrae* are restored in part. Because of this and some distortion it is not possible to give exact dimensions. It is thought, however, that the greatest diameter was not over 120 mm.

The *supratemporal fenestrae* show a development similar to that of *Mystriosuchus*.<sup>1</sup> The posterior border, i.e., the parieto-

<sup>1</sup> J. H. McGregor, "The Phytosauria, with Especial Reference to *Mystriosuchus* and *Rhuidodon*," *Mem. Am. Mus. Nat. Hist.*, Vol. IX (1906), Part II.

supramasal arcade is markedly depressed. The depression of this arcade has not advanced so far as in *Machaeroprotopus validus*.<sup>1</sup> The opening is very inconspicuous in a superior view because of the backward extension of the postorbital. The opening is directed out and back. It is slitlike, but its length cannot be determined because the outer posterior border is missing.

#### SEPARATE BONES OF THE DORSAL ASPECT

The *premaxillae* are gradually expanded laterally at the anterior ends for the accommodation of the large terminal teeth. The expanded portion is abruptly down-curved and extends about 30 mm. below the palate surface of the rostrum. At the margins of jaw, the premaxillae unite with the maxillae at about the twenty-fifth tooth. From this point the suture extends back and up in an irregular line. At the median line each premaxilla sends back a process to within 45 mm. of the nares. This process and a lateral posterior process extending back the same direction clasp the anterior process of the septomaxilla.

The *septomaxillae* are larger than in any other form that the writer has examined. They are united along the median line for a distance of 48 mm. and thence extend forward between the posterior process of the premaxillae a distance of 45 mm. The septomaxillae form a large area about the front and sides of the narial prominence, but their exact posterior extent cannot be determined. It is thought that they make up but a small part of the narial septum.

The *maxilla* has its greatest anteroposterior extent along the alveolar margin. In this respect it differs from the University of Wisconsin specimen referred to above.

The *nasals* form the posterior, median, and most of the lateral border of the nares. The lower anterior margin extends some distance beyond these openings, essentially as far as the septomaxillae. Posteriorly they extend about 35 mm. beyond the posterior border of the antorbital vacuity.

In the shape and extent of the *lachrymals* and *prefrontals* there is the normal phytosaur development.

The *parietals* differ from those of *Machaeroprotopus validus*<sup>2</sup> in

<sup>1</sup> Mehl, *op. cit.*, p. 8, Fig. 2.

<sup>2</sup> *Ibid.* p. 11.

that their combined width is equal to the interorbital width. Their length is 67 mm. and combined width the same.

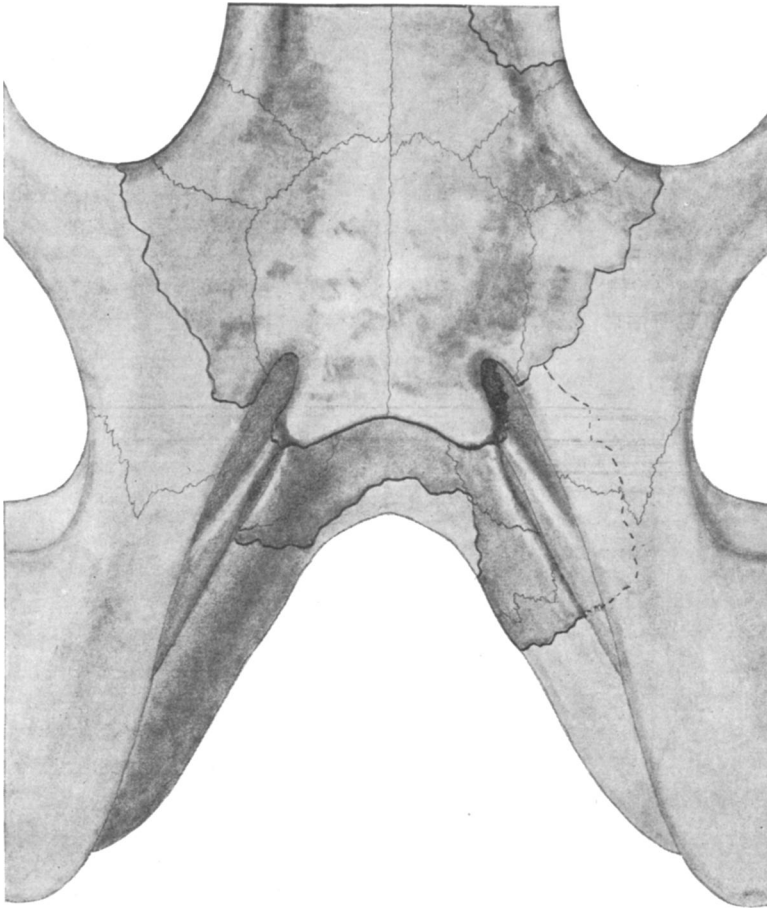


FIG. 2.—*Machaeroprotopus andersoni*, details of the posterior end of the skull as seen from above. Restored portions are indicated by lighter shading and less heavy outlines. Two-thirds natural size.

The *postfrontals* are small and make but a small part of the orbit boundary, as is usually the case.

The relation of the *postorbitals* is not clearly shown. The posterior extent of these bones cannot be determined, for that portion of the skull is restored.



ings are evident in a comparison of Figure 2 with that of *M. validus*.<sup>1</sup>

#### THE PALATE

The palate of this specimen (Fig. 3) seems very little distorted, but although the configuration of the bones is readily determined, some of the sutures are obscure. The bones are thin and overlapping, and the slightest abrasion tends to obliterate the unions.

The palate is marked by the characteristic phytosaurian ridges just within the alveolar border. These start indistinctly near the third tooth back of the down-turned terminus of the rostrum and increase in prominence to a point a little in advance of the internal nares. From here they flatten out posteriorly and lose their identity before the last tooth is reached. A slight median ridge, low and rounded, continues forward from the internal nares to about mid-length of the rostrum.

In the region of the twenty-third tooth, there is a conspicuous lateral expansion or swelling of the rostrum. The alveolar ridges broaden in this region to fill in the increased width.

Among the most striking features of the palate is the development of the narial arch. In *Angistorhinus*,<sup>2</sup> from the slight arching formed by the alveolar ridges far forward, the height increases gradually until it is broad and marked just in front of the nares. Here the height increases rapidly to about 42 mm. at the posterior end of the nares. At this point the arch has a width of 82 mm. In this genus there is not the slightest suggestion of the constriction of the arch at the lower palate plane, the suggestion of a primitive false palate.

In *Mystriosuchus*, as McGregor has shown,<sup>3</sup> the constriction of the narial arch at the lower palate plane is marked. To quote:

This arched condition of the palate suggests two questions of great importance in their bearing upon the genetic relationships of the group, namely: (1) Do the Phytosauria exhibit the incipient formation of a secondary palate? and (2) if so, is this the first step in a phyletic series, culminating in the highly

<sup>1</sup> Mehl, *op. cit.*, p. 8, Fig. 2.

<sup>2</sup> M. G. Mehl, "The Phytosauria of the Trias," *Jour. Geol.*, Vol. XXIII (1915), No. 2, pp. 129-65.

<sup>3</sup> McGregor, *op. cit.*, pp. 42-43.



modified palate of the eusuchian crocodiles? As for the first of these questions I feel that there is no escape from an affirmative answer; an examination of the palate of either *Mystriosuchus* or *Phytosaurus* [*Lophoprosoopus*] shows a pair of longitudinal palatine ridges . . . which plainly represent the beginnings of a secondary palate. . . .

The rounded inner border [of the portion of the palatine about the base of the narial vault] projects very slightly toward the middle line, so that the palatal aspect of the cranium exhibits two elongate ridges which approximate each other within 25 mm. at the level of the anterior border of the nares, diverging gradually behind this region. These palatine ridges partly obscure the outer part of the narial cavities and are continued anteriorly on the maxillaries, but fade out posteriorly without involving the pterygoid. . . . It should be explained that these ridges do not present a sharp edge, but are broadly rounded. Nevertheless it is an approximation of the palatines, ventral to the internal nares and the pterygoids, and it seems to me that it must be interpreted as a *tendency* toward the formation of a secondary palate. . . .

In the present form this tendency is so marked that there can be no doubt as to its meaning. The narial vault has its greatest width somewhat back of the nares. The cavity is still partly filled with matrix, but is at least 80-90 mm. wide and somewhat over 50 mm. high. So restricted is the arch at the lower palate plane by the median extension of the palatines, that the opening as seen in a palate view is little more than a slit, not over 24 mm. wide near the posterior border of the nares and gradually widening to the region of the interpterygoid vacuities. This constriction in the narial region is in the form of sharp-edged, thin, horizontal plates extending beneath the narial vault at the plane of the palate. The suggestion of an unfinished or rough edge bespeaks a cartilaginous or fleshy continuation. It is believed that the air passage was thus completely closed below for a considerable distance back of the nares.

The alveolar ridges cannot be considered as part of this "false palate," as is suggested by the foregoing quotation. In the present form they are quite distinct from the palatine extensions beneath the nasal vault. These alveolar ridges, always conspicuously developed in the phytosaurs, should probably be looked upon as buffers to prevent the breaking or interlocking of the teeth through the sharp snapping of the jaws in an unsuccessful attempt at seizing prey.

## OPENINGS OF THE PALATE

The length of the *internal nares* is 71 mm., about 8 mm. greater than that of the external openings. The internal nares are about 20 mm. in advance of the externals at their posterior border.

The *postpalatine foraminae* are exceptionally small and inconspicuous. They are, in fact, little more than slight depressions or cracks along the palatine-ectopterygoid union. They are not over 30 mm. long and if actually perforating the palate are not more than 3 mm. wide.

The *interpterygoid openings* are exceptionally small. Their exact anteroposterior extent cannot be determined, but they could have been but little more than 25 mm. long.

## THE BONES OF THE PALATE

Some of the details of the relations of the bones of the palate are not at all certain. In the palate restoration, the writer has attempted to show the relation as the weight of the evidence seems to indicate and not as indisputably determined.

The *premaxillae* apparently have a remarkable posterior extent on the palate surface. They seem to form the anterior border and the entire inner boundary of the internal nares and extend a short distance back of these openings along the median line. An unpublished drawing of this specimen by S. W. Williston doubtfully places the posterior end of the premaxillae about 40 mm. in front of the internal nares. The bone in this region is platy and brittle and has been somewhat abraded in preparation. The writer recognizes the possibility of the premaxilla-vomer suture in this region, but cannot verify this point.

The *maxillae* extend forward on the palate surface to the twenty-fourth tooth, numbering from the front. Their width on the palate is at no place much greater than that required for the alveolar ridges. The union with the jugal as seen in a palate is not determinable.

The *vomers* seem to be exceptionally small and confined to the posterior and possibly the posterolateral borders of the internal nares. This is a condition decidedly unlike that usually attributed to the phytosaurs and is merely suggested. What is assumed to be

the union of the premaxillae and the vomer at the inner posterior border of the nares may be a fracture. If so it is remarkable for its symmetry in relation to the median line of the skull. Of the posterior boundary there can be little doubt. It joins the pterygoid in a forward convex line about 32 mm. back of the internal nares.

The *palatines* apparently form a goodly portion of the lateral borders of the internal nares. Aside from this, however, they seem to be largely confined to the lower palate plane. It is thought that their union with the pterygoids and vomers is at or near the base of the narial vault, but of this one cannot be sure because of the matrix-filling part of the cavity. Posteriorly the palatines come to an acute angle, the point of which prevents the articulation of the pterygoids with the ectopterygoids on the palate surface.

The *ectopterygoids* are small, triangular bones. The posterior borders are down-curved so as to be conspicuous in a lateral view of the skull.

The *pterygoids* are exceptionally large, but are almost entirely confined to the sides and roof of the narial arch. Their extent along the pterygo-quadrato bar cannot be determined.

The *parasphenoid* has been destroyed, but it must have been very similar to that shown in the palate restoration. The union between the *basi-sphenoid* and the *pterygoids* and *basi-occipital* is as indicated in the restoration. The relation of the other bones of the posterior part of the skull as seen in the palate view cannot be determined. The relations shown are those determined from the University of Wisconsin specimen mentioned above.

#### THE TEETH

With the exception of a few roots and one partially erupted tooth in the middle of the series that shows the crown, all the teeth have been lost. The alveolar margin of the jaw is splendidly preserved for the most part and gives a good indication of the number of the teeth and of their variations in size.

The alveolae are all distinct and usually separated by a space of at least 3 to 5 mm. In each maxilla there are apparently twenty-four teeth and twenty-three in each maxilla, a total of ninety-four

in the upper dentition. In the downward portion proper of the premaxilla there are two alveolae of a size and shape to indicate long conical teeth of about 21 mm. diameter at the base. Immediately behind the down-turned portion is another large alveolus, about 15 mm. in diameter. This is followed closely by a fourth, considerably smaller, alveolus. Between the fourth and fifth alveolae is a conspicuous space. This is marked on one premaxilla by a depression as though for the reception of a tooth from the lower jaw. The following alveolae, with the exception of the last few on the premaxilla, increase gradually in size from about 6 mm. to 12 mm. There is a marked lateral expansion of the rostrum near the posterior end of the premaxillae for the accommodation of three or four exceptionally large teeth. The root of one of these is preserved and measures 13 mm. in diameter. The crown preserved in the maxilla series as mentioned above is laterally compressed with sharp, slightly serrate, anterior and posterior edges.

It would seem that the dentition was very much like that of *Machaeroprotopus validus*,<sup>1</sup> greatly enlarged seizing teeth in the front, grading through smaller, sharp, conical to laterally compressed slicing teeth behind. The space between the fourth and fifth alveolae indicates likewise a shorter jaw with large terminal teeth directed sidewise.

#### RELATIONSHIPS AND HABITS

Of the close affinity between the present specimen and that described as *Machaeroprotopus validus*<sup>2</sup> there can be no doubt; both skulls are crested forms of the "broken outline" type; both have the depressed posterior border of the supratemporal openings; and both have enlarged, conical terminal teeth with laterally compressed, sharp-edged, slicing teeth behind. The skulls differ in so many minor points, however, that they can scarcely be placed in the same species. The writer will designate the present form, therefore, as *Machaeroprotopus andersoni* in honor of Professor Anderson, who presented the material to the University of Chicago.

<sup>1</sup> Mehl, *Bull. Univ. of Oklahoma, op. cit.*, p. 20.

<sup>2</sup> *Ibid.*

The following table comparing the two forms will show the chief differences on which the new species is established.

<i>Machaeroprotopus validus</i>	<i>Machaeroprotopus andersoni</i>
Postero-median border of supra-temporal fenestrae completely depressed.	Postero-median border of supra-temporal fenestrae not completely depressed.
Anterior border of nares elevated above lateral borders.	Anterior border of nares not elevated.
Terminal expansion of rostrum abrupt.	Terminal expansion of rostrum gradual.
Nasals not extending to anterior border of nares.	Nasals extending some distance in front of anterior border of nares.
Greatest length of maxillae above alveolar margin.	Greatest length of maxillae at alveolar margin.
Approximately seventy-four teeth in upper dentition.	Approximately ninety-four teeth in upper dentition.
Six large teeth in terminal expansion of rostrum.	Four large teeth in terminal expansion of rostrum.
Alveolae crowded, occasionally confluent.	Alveolae not crowded.
No lateral expansion of rostrum at posterior end of premaxillae.	Lateral expansion of rostrum at posterior end of premaxillae.

The Phytosauria are a unified group in that they all tend to develop certain peculiarities that set them off from other groups in a striking manner. All developed the snoutlike elongation of the skull, an elongation that left the nares far from the tip. In some cases there seems to have been an actual retreat of the nares. There seems also to have been a tendency to elevate the nares above the plane of the cranium proper, a goal very conspicuously reached in several forms. All of the phytosaurs showed a more or less marked development of greatly enlarged terminal teeth and most of them developed at least a crude slicing dentition farther back in the jaws.

These modifications or tendencies are so distinctive that they have called forth considerable speculation as to the habits of the

phytosaur. The seemingly common goal in the modifications of all the phytosaurs suggests similar habits. Of the probable habits of *Machaeroprotopus* the writer has stated in another place:<sup>1</sup>

All of the phytosaurs were supposedly more or less amphibious in habit. Still, the heavy dermal armor of several of the forms would indicate that a very considerable part of their time was spent on the land. The posterior position of the nares is usually not considered a distinct aquatic adaptation in the case of the phytosaurs. It is rather explained, along with the long snout and large terminal teeth, by attributing to the slender rostrum the function of a prod or rake with which the possessor searched out worms and other soft bodied invertebrates, etc., in the mud of shallow waters while the nares, by virtue of their position, were above the surface of the water.

There is a marked tendency in most of the phytosaurs, a tendency in which *M. validus* surpasses all other known forms, for the nares to rise on a considerable prominence. This would seem to be a modification entirely uncalled for were the position of the nares due solely to the use of the rostrum as a prod. So situated are the nares in *M. validus* that it could submerge the body save for the narial hump and lie in wait admirably concealed from its enemies, or more likely, from its prey. Certainly the teeth of this form are more fitted for tearing large vertebrates than for small, mud-burrowing creatures. Then too, *Machaeroprotopus* could scarcely pick small objects from the ground because of the difference in length between the upper and lower jaws. When the jaws were closed the terminal teeth of the lower jaw were functionless and the upper terminal teeth were but little better. It was not until the jaws were wide open that the terminal teeth could be used effectively either as a rake or for seizing any sort of prey. With the jaws separated, however, the upper and lower terminal teeth were directly opposed and admirably fitted for seizing and tearing large animals. It seems likely that *M. validus* was wont to lie in wait concealed close up to the shore in shallow waters ready to seize its prey when the latter came down to drink. Once the prey was dragged into the water it was at the mercy of its captor, for the dentition of the latter probably matched that of any carnivorous land form of the time and the phytosaur had the distinct advantage of being entirely at ease in the water.

If these were the habits of the more highly specialized phytosaurs, and the assumption seems logical, the group was remarkably well adapted to the conditions of the times. The adaptation was, moreover, of a very peculiar nature. In most cases adaptations seem to do little more than tend to counteract adverse conditions. For instance, the development of speed in ambulatory forms of

<sup>1</sup> Mehl, *Bull. Univ. of Oklahoma, op. cit.*, pp. 23-24.

arid regions permits a wider range about the limiting water supply to compensate for the diminished food supply and the distance between water-holes.

In *Machaeroprotopus* the modifications not only met an emergency but actually turned it to advantage; the phytosaur waited for the rigorous conditions to bring his food within reach. If our interpretation of the conditions in the western interior of North America during Triassic times is correct the scarcity of food necessitated a wide range for many forms. This meant speedy forms ordinarily difficult of capture, but it also meant the periodic crowding of the limited water-holes; it compelled the food to walk to the captor.

It is not easy to see why a group so remarkably fitted to their environment as was the phytosaur group should not prosper better as a race. They were very short lived, confined to the latter part of the Trias, apparently. One can scarcely appeal to *overspecialization* unless this means "fitting in" rather than marked structural change. The phytosaurs were scarcely less generalized than the living crocodilians. Perhaps *perfection* alone is enough to condemn a race. A consideration of this possibility will form the basis for a future paper.